

AN ANALYSIS OF MORPHOLOGICAL VARIATION IN *MUHLENBERGIA CAPILLARIS* (POACEAE) AND ITS ALLIES IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Muhlenbergia capillaris and its allied species, *M. expansa* and *M. filipes* have been variously classified in the past as three distinct species or a single species with three varieties. A numerical analysis was performed on data taken from herbarium specimens collected throughout the geographic distribution of these taxa. Analysis of variance, principal components analysis, cluster analysis, and discriminate analysis indicate there is a continuum of morphological variation present. A single species with three varieties (var. *capillaris* var. *filipes* and var. *trichopodes* is recognized. A key to the varieties and descriptions of each are presented.

INTRODUCTION

Muhlenbergia capillaris (Lam.) Trin. and its related taxa, *M. filipes* M. A. Curtis and *M. expansa* (DC.) Trin., are common species found along rocky or sandy woodlands, pine barrens, and coastal sand dunes throughout the southeastern United States. This group can readily be identified in the field by the large bunchgrass appearance, long leaf blades (flat or involute), large wide spreading panicle, and long narrow (usually purple) spikelets with a single floret.

In the extremes of their variation, each taxon appears to be a well defined species. The primary characters which have been used to separate them are the length of the lemma awn and glume awns, relative length of the glumes to the floret, and the degree to which the leaf blade is involute. Several authors have noted a large amount of variation within each taxon. Vasey (1892) reduced *M. expansa* to a variety of *M. capillaris* (var. *trichopodes* based on *M. trichopodes* Chapm.). However, Hitchcock (1935) did not follow this treatment and maintained *M. expansa* as a distinct species. More recent taxonomists have followed this treatment (Fernald 1950; Hitchcock

1951; Gleason and Cronquist 1963; Radford, et al. 1968; Reeder 1975) with few dissenters (Correll and Johnston 1970). Reeder (1975) suggested a possible distinction between *M. capillaris* and *M. expansa* noting the basal leaves of the latter often become fibrous at maturity. *Muhlenbergia filipes* was reduced to a variety of *M. capillaris* by Beal (1896) upon the suggestion of Chapman accompanied by no discussion. This treatment has been followed by most recent authors (Hitchcock 1935; Fernald 1950; Hitchcock 1951; Radford, et al. 1968; Correll and Johnston 1970). However, further morphological and phenological studies by Pinson and Batson (1971) suggested that this taxon deserved specific recognition. This has since been followed by Reeder (1975).

While preparing a treatment of the genus *Muhlenbergia* for the *Vascular Flora of the Southeastern United States* we examined many specimens that did not correspond to previously described morphological limits of the taxa in this complex. The purpose of this study was to perform a phenetic analysis of morphological data representing this complex to determine whether specific recognition of these taxa is warranted. The criteria used in making this determination will be based on the presense or absence of morphological discontinuities.

MATERIALS AND METHODS

Herbarium specimens from 25 herbaria located primarily in the southeastern United States were observed. Of these, 350 specimens were selected from across the geographic distribution of the complex and measured for 15 variable morphological characters. Spikelet measurements were made using a dissecting microscope with an ocular scale calibrated to 0.1 mm. Culm length and inflorescence length were measured separately such that culm length did not include inflorescence length. The plant base was recorded as a present or absent character: '1' if basal sheaths were fibrous, and '0' if not fibrous.

Two methods were used to analyze the variation present among the morphological characters. Statistical Analysis System, or SAS (Goodnight 1979) was used to provide basic statistical data and to perform discriminant analysis. The Numerical Taxonomy System of Multivariate Statistical Programs (NTSYS; Rohlf, et al. 1980) was utilized to provide principal components analysis (PCA) and cluster analysis of the data. Cluster analyses were performed with UPGMA and distance matrices.

RESULTS

Table 1 lists the range, mean, and standard deviation of the characters measured for each of the three taxa analyzed. Two analyses were run of both

Character	<i>capillaris</i>			<i>expansa</i>			<i>filipes</i>		
	range	mean	sd	range	mean	sd	range	mean	sd
Culm length•	12-110	51.0	17.4	22-100	54.0	16.6	23-92	54.0	17.3
Culm width*	0.7-3.2	1.6	0.4	0.9-3.3	1.6	0.4	1.1-3.4	2.2	0.5
Plant base	0-1	0.25	0.4	0-1	0.85	0.4	0-1	0.08	0.3
Leaf blade length•	11-80	28.0	11.1	10-47	24.0	8.7	14-75	36.0	15.2
Inflorescence length•	15-57	32.0	7.8	15-50	30.0	6.5	15-50	33.0	7.4
Inflorescence width•	5-25	13.0	4.0	3-41	9.0	4.5	6-23	12.0	3.4
Pedicel length*	3-46	19.4	7.2	2-37	14.0	6.6	8-48	20.3	8.5
Spikelet length*	2.5-4.6	3.4	0.4	2.7-5.1	3.8	0.6	2.4-4.8	3.7	0.5
First glume length*	0.3-2.3	1.3	0.4	1.1-3.6	2.5	0.5	0.5-1.7	1.0	0.3
First glume awn length*	0-3.2	0.2	0.5	0	0.0	0.0	0-10.3	3.3	2.6
Second glume length*	0.3-2.4	1.3	0.4	1.3-4.1	2.7	0.6	0.6-2.1	1.2	0.3
Second glume awn length*	0-5.0	0.6	1.0	0-0.6	0.0	0.1	1-25	11.2	6.0
Lemma length*	2.4-4.4	3.3	0.5	2.6-5.0	3.6	0.5	2.3-4.7	3.6	0.5
Lemma awn length*	0-17	6.6	3.5	0-4.0	0.7	0.7	8-33	17.7	4.3
Setaceous teeth length*	0-2	0.1	0.3	0-0.1	0.0	0.0	0-4.5	1.7	1.1

TABLE 1. Range, mean, and standard deviation (sd) for the three taxa for each characters used in the numerical analysis. An asterisk (*) indicates those characters measured in millimeters; a bullet (•) indicates those characters measured in centimeters.

the PCA and cluster analysis. The first analysis used all 15 characters, the second used only characters that had most of their variation explained by a significant principal component 1 or 2. In the first principal components analysis, principal component 1 identified first glume awn length, second glume awn length, lemma awn length, and length of setaceous teeth as the main characters contributing to the clustering, and principal component 2 identified spikelet length, first glume length, second glume length, and lemma length. However, the correlation for this analysis was quite low ($R = -0.37$) and the first two components accounted for only 48.6% of the variation. Results of the second PCA (Fig. 1) show a pattern similar to that

of the first PCA although the pattern is more tightly clustered. As shown, the variation among specimens analyzed is continuous (Fig. 1). The correlation coefficient in this second analysis was much higher ($R = -0.73$) and the first two components accounted for 75% of the variation present.

The cluster analysis based on the eight characters identified by principal components 1 and 2 is presented as a distance phenogram in figure 2. Only the major groupings of the phenogram are presented. Six major groupings were identified (F_1 , F_2 , $C + F$, C , $C + E$, and E) with approximately 30% of the OTU's falling into mixed groups. It was possible by observation of the data set to determine what character states comprised each of the groups in the cluster analysis. For example, group F_1 is composed of specimens with glume awn length exceeding 15 mm, lemma awn length exceeding 20 mm, and setaceous teeth of the lemma 1.5 – 2.5 mm long, where in group F_2 the specimens have moderate length glume awns, variable to long lemma awns and setaceous teeth at least 3 mm long.

That a proportion of specimens were clustered into mixed groups was substantiated by a test of discriminant analysis. An *a priori* designation was assigned to each specimen to test the classification using discriminant analysis. Thirteen specimens were evaluated as misclassified, primarily from the *filipes* to *capillaris* or *expansa* to *capillaris* form. The classification for those specimens identified was modified and the test rerun with a similar result, 12 different specimens were evaluated as misclassified.

DISCUSSION

As shown in Table 1, there is an overlap in the morphological range of the diagnostic characters used in past treatments. Because of this variation, it is often difficult to identify specimens. Many specimens have several characters that may fit the range of different taxa. The resulting identification of such specimens can only be based on the subjective correlation of characters. The possibility also exists that these specimens represent putative hybrids.

Several of the characters warrant further elaboration. Reeder (1975) used basal sheaths becoming fibrous at maturity in *M. expansa* as an important distinguishing character. However, the results here indicate that 25% of *M. capillaris* and 8% of *M. filipes* specimens had fibrous basal sheaths at maturity. The degree to which the sheaths became fibrous varied considerably and specimens characteristic of *M. expansa* tended to have a more pronounced fibrous nature. However, there is little evidence to support this character in maintaining species boundaries.

The setaceous teeth of the lemma were identified as an important charac-

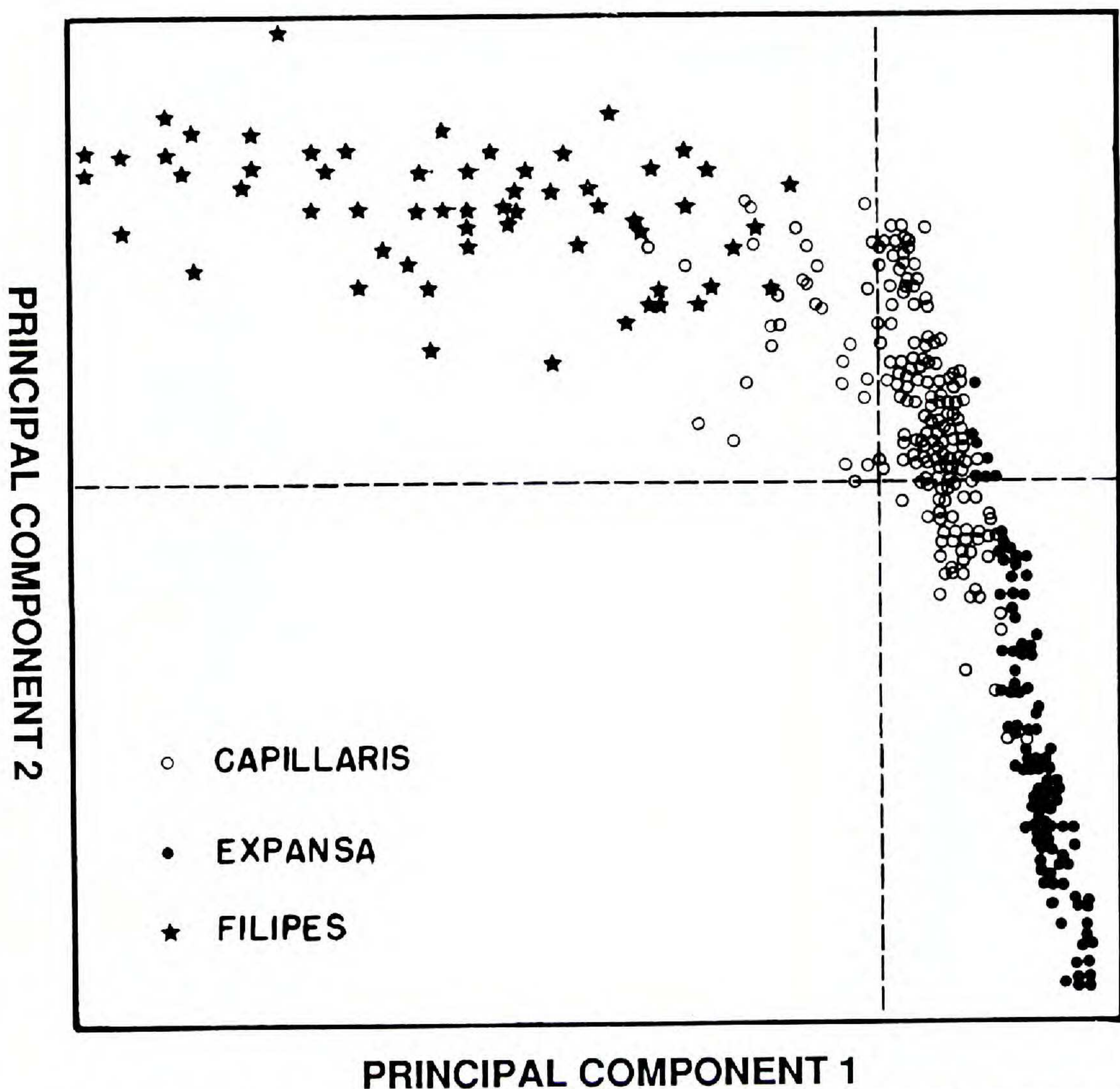


FIG. 1. Principal components analysis using eight characters identified by principal components 1 and 2 as significantly accounting for the variation present in initial analysis. $R = -0.73$, and components 1 and 2 accounted for 75% of the variation.

ter in separating *M. filipes* from *M. capillaris* by Pinson and Batson (1972). They reported that the lemma of *M. capillaris* did not have setaceous teeth, yet in this study specimens referable to *M. capillaris* based on glume and lemma awn length had setaceous teeth as long as 2 mm. This is by no means common within the complex, yet it does occur with enough frequency that it cannot be regarded as an occasional phenomenon. Also, examination of the type fragment of *Stipa capillaris* (US) reveals the presence of setaceous teeth to 0.8 mm long.

It is evident from these analyses that there is no clear separation of the taxa. Principal components analysis shows a continuum of morphological variation from one extreme to the other, and neither cluster analysis nor

discriminant analysis could adequately separate the three taxa. Because of the lack of morphological discontinuity between the taxa it is our opinion that this complex is represented by a single species. However, because the statistical analyses were able to identify several broadly classified groups and some phenological differences between the forms has been previously noted (Pinson and Batson 1971), we recognize three varieties within this morphologically variable species.

Currently, no information is known concerning the chromosome number of these taxa and little is known regarding the anatomical variation present. Kearney (1900) compared the leaf cross sections of members of this complex and concluded that distinctions based on leaf anatomy were evident. Morden and Hatch (1987) have previously shown that distinctions among species based on anatomical differences are possible within some groups of species in *Muhlenbergia*. Future research with this group should be directed toward understanding the genetic relationships among these taxa in addition to the anatomical and epidermal variation that appears to be present.

TAXONOMY

MUHLENBERGIA CAPILLARIS (Lam.) Trin., Gram. Unifl. 191. 1824.

Densely caespitose perennial; culms simple, erect, 6–10 (15) dm tall, 0.7–3.4 mm diam., glabrous or puberulent below the nodes. Sheaths rounded, glabrous, basal sheaths often becoming fibrous at maturity. Ligule firm, strongly decurrent, 2–5 mm long on lower blades, up to 10 mm long on upper blades. Blades flat or involute, elongate, 10–80 mm long, 2–4 mm wide, curved outward at base, veins tan, midvein not prominent, abaxial surface glabrous or with infrequent pilose hairs, adaxial surface densely scabrous. Inflorescence an open panicle, base often included in the leaf sheath, 15–50 (60) cm long, 5–30 (40) cm wide, narrow when immature and spreading at maturity. Spikelets acuminate, 2.4–5.1 mm long, purple or occasionally green, brown, or yellowish, subsessile or on pedicels up to 5 cm long. Glumes subequal, acute, awned or awnless, first glume 1-nerved, second glume 1–3-nerved. Lemma awned or awnless, usually purple or green, 2.3–5.0 mm long, 3-nerved, nerves often obscure, apex acuminate, puberulent on callus, scabrous near apex. Palea shorter to slightly longer than lemma, 2.1–4.5 mm long, glabrous or scabrous between the nerves. Anthers purple, 1.5–2.0 mm long. Caryopsis 2–2.5 mm long, dark brown, narrowly elliptic. Embryo ca. 1/2 the length of the caryopsis.

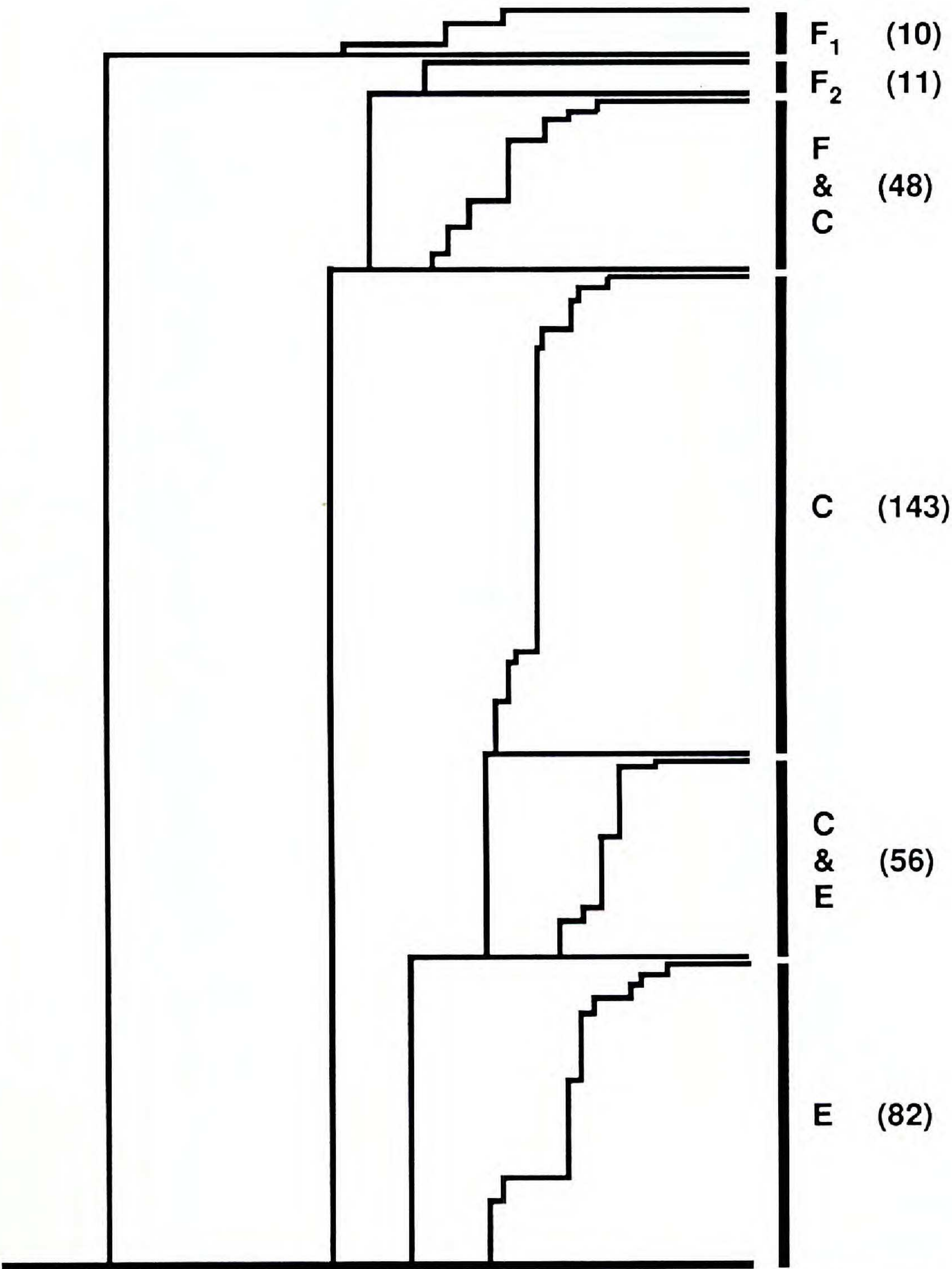


FIG. 2. Cluster analysis using eight characters identified by principal components 1 and 2 as significantly accounting for the variation present in initial analysis. C, E, and F represent forms which would be referred to the taxa *M. capillaris*, *M. expansa*, and *M. filipes*, respectively. The numbers in parenthesis represents the number of OTU's in each group.

KEY TO THE VARIETIES OF *Muhlenbergia capillaris*

- Glumes less than 1/2 length of lemma; lemma awn longer than 3 mm, seldom awnless.
 Glume awns 0–4 mm long; lemma awn 2–13 (18) mm long; lemmas without conspicuous setaceous teeth 1. var. *capillaris*
 Glume awns 2–25 mm long, when less than 5 mm then lemma awn greater than 20 mm long; lemma awn 8–33 mm long; lemma with conspicuous setaceous teeth 1–5 mm long 2. var. *filipes*
 Glumes greater than 1/2 length of lemma; lemma usually awnless or with short awn to 3 mm long 3. var. *trichopodes*

1. var. CAPILLARIS

- Stipa capillaris* Lam., Tabl. Encycl. 1:158.1791. TYPE: Carolina, *Fraser s.n.* (P, US fragment!). *Podosemum capillare* (Lam.) Desv., Nouv. Bul. Soc. Philom. 2:188. 1810. *Trichochloa capillaris* (Lam.) DC., Cat. Hort. Monsp. 152. 1813. *Agrostis setosa* Willd. ex Trin., Acad. St. Petersb. Mem. VI Sci. Nat. 4(1):300. 1841, as synonym of *Stipa capillaris*.
Stipa diffusa Walt., Fl. Carol. 78. 1788 (not *M. diffusa* Willd.)
Stipa sericea Michx., Fl. Bor. Amer. 1:54. 1803. TYPE: South Carolina, *Michx. s.n.* (P, US fragment!). *Agrostis sericea* (Michx.) Ell., Bot. S.C. and Ga. 1:135. 1816. *Polypogon sericeus* (Michx.) Spreng., Syst. Veg. 1:243. 1825. *Stipa cericea* Michx. ex Raf., Neogen. 4. 1825, error for *Stipa sericea*.
Tosagris agrostidea Beauv., Ess. Agrost. 29 (as *T. agrostidea*) pl. 8, f. 3 (as *T. agrostidea*). 1812. TYPE: United States. *Podosemum agrostideum* (Beauv.) Beauv., Ess. Agrost. 176. 1812. *Podosaemon agrostideum* (Beauv.) Beauv. ex Spreng., Syst. Veg. 1:243. 1825.
Trichochloa polypogon DC., Cat. Hort. Monsp. 152. 1813. TYPE: Carolina, *Fraser s.n.* (P, US fragment!). *Muhlenbergia polypogon* (DC.) Kunth, Rev. Gram. 1:64. 1829.
Trichochloa purpurea Beauv., Ess. Agrost. 29. pl. 8. f. 2. 1812. TYPE: United States. *Podosemum purpureum* Beauv., Ess. Agrost. 176. 1812.
Trichochloa expansa DC., Cat. Hort. Monsp. 151. 1813. TYPE: Carolina, *Bosc s.n.* (P, US fragment!). *Agrostis rubicunda* Bosc ex DC., Cat. Hort. Monsp. 151. 1813, as synonym of *T. expansa* DC. *Muhlenbergia expansa* (DC.) Trin., Gram. Pan. 26. 1826.
Muhlenbergia caespitosa Chapm., Bot. Gaz. 3:18. 1878. TYPE: Florida. Apalachicola, *Chapman s.n.*

Basal sheaths often fibrous although not extensively so; glumes subequal, 1/4–1/2 the length of the spikelet, first glume awn 0–3 mm long, second glume awn 0–5 mm long; lemma occasionally with setaceous teeth at apex to 1 mm long, awn (0) 2–18 mm long; palea usually awnless. Common in rocky or sandy woodlands from Massachusetts to Illinois, south to Oklahoma and east Texas and Florida. Also reported from eastern Mexico and the West Indies. Flowering late August to November.

NOMENCLATURE.—A fragment of *Stipa capillaris* Lam. is at US and clearly shows the glumes with awns 2–4 mm long and setaceous teeth of

the lemma 0.2 – 0.8 mm long. A fragment of *Stipa sericea* Michx., also at US, has written on the sheet “glumes minute, delicate awned as var. *filipes*” in Hitchcock’s script. The spikelets, however, closely resemble that of *Stipa capillaris* Lam. except that the glumes are truncate or erose at the apex. The illustration of *Tosagris agrostidia* in Beauvois’ *Essai Agrostographie* (1812) is var. *capillaris*. Beauvois’ illustration of *Trichochloa purpurea*, long considered a synonym of var. *trichopodes*, is a form of var. *capillaris* with awnless glumes and short awns on the lemma, the glumes being less than 1/2 the length of the floret. A fragment of *Trichochloa expansa* DC. at US is also var. *capillaris*, the glumes ca. 1/3 the length of the floret and the lemma short awned. It is apparent that de Candolle and Poiret (for *Stipa expansa*) were describing two different specimens, both collected by Bosc in “Carolina.” De Candolle (1813) doubtfully cited Poiret, stating that the spikelet of *T. expansa* had short glumes, whereas Poiret mentioned that the glumes almost equal the floret. De Candolle stated that there may have been a typographical error in Poiret’s work. However, this is probably not the case. In transferring this taxon to *Muhlenbergia*, Trinius (1826) cited *Trichochloa expansa* DC. as the basionym and excluded as a synonym Poiret’s name indicating he did not choose to recognize it. His Latin diagnosis also correlates with that of de Candolle’s. See also nomenclature of *Stipa expansa* Poir. under var. *trichopodes*. A fragment of *Trichochloa polypogon* DC. at US is also a form of var. *capillaris* with glumes and lemma short awned. The description by Chapman (1878) of *Muhlenbergia caespitosa*, floret “...four times as long as oval, obtuse, or denticulate glumes and equalling the stout rough awn,” clearly allies this with var. *capillaris*. The location of the type of *Stipa diffusa* Walt. is uncertain and Walter’s (1788) description is vague. It has been placed in synonymy with var. *capillaris* by others (Hitchcock 1951), and we will retain it there until such time as the type can be observed.

2. var. *FILIPES* (M. A. Curtis) Chapm. ex Beal, Grasses N. Amer. 2:256. 1896.

Muhlenbergia filipes M. A. Curtis, Amer. J. Sci. 44:83. 1843. TYPE: Sea Islands of North Carolina, *Curtis s.n.* (SYN: GH!, MO!, NY, US fragment!). *Podosemum filipes* (M. A. Bush, Amer. Midl. Nat. 7:29. 1921.

Basal sheaths rarely fibrous; glumes subequal, about 1/4 the length of the spikelet, conspicuously long-awned, first glume awn usually shorter than second, 0 – 10 mm long, second glume awn 3 – 25 mm long; lemma with two setaceous teeth at apex, occasionally arising from the awn above the lemma, awns 10 – 35 mm long, rarely shorter; palea nerves often exten-

ding as awns up to 2 mm long. Sand dunes and coastal woodlands from North Carolina south to Florida and west to East Texas. This variety tends to be more robust in all characters. Flowering September to December, occasionally January.

NOMENCLATURE.—The type of *M. filipes* M. A. Curtis at GH, MO, and US is long awned from the glumes, lemma, and palea. The setaceous teeth of the lemma are 1–2 mm long and appear to come off the awn column rather than the lemma apex.

3. var. *TRICHOPODES* (Ell.) Vasey, Contr. U.S. Natl. Herb. 3:66. 1892.

Stipa expansa Poir. in Lam., Encycl. Meth. 7:453. 1806. TYPE: Carolina, *Bosc s.n.* (P?).

Agrostis arachnoidea Poir. in Lam., Encycl. Suppl. 1:249. 1810. TYPE: Carolina, *Bosc s.n.* (P, US fragment!). *Vilfa arachnoidea* (Poir.) Beauv., Ess. Agrost. 147, 181. 1812. *Cinna arachnoidea* (Poir.) Kunth, Rev. Gram. 1:67. 1829. *Muhlenbergia arachnoidea* (Poir.) Trin. ex Kunth, Enum. Pl. 1:207. 1833. *Agrostis expansa* Poir. ex Steud., Nom. Bot. ed. 2. 1:40. 1840. *Agrostis longiflora* Willd. ex Steud., Nom. Bot. ed. 2. 1:41. 1840.

Agrostis trichopods Ell., Bot. S.C. and Ga. 1:135. pl. 8. f. 1. 1816. TYPE: Chatham Co.: near Charleston, Ga., *Baldwin s.n.* (CHARL). *Muhlenbergia trichopodes* (Ell.) Chapm., Fl. South. U.S. 553. 1860. *Podosemum trichopodes* (Ell.) Bush, Amer. Midl. Nat. 7:30. 1921.

Basal sheaths very fibrous or not; glumes subequal, awnless or the second occasionally mucronate; lemma awnless or with a short awn to 3 mm long, setaceous teeth absent; palea awnless. Moist, sandy pine forest near the coast from Virginia south to Florida and west to East Texas. Flowering August to late October.

NOMENCLATURE.—Weatherby (1942) indicated that the type of *Agrostis trichopodes* is still present in Elliott's herbarium although it was not available for this study. Elliott's description (1816), however, seems conclusive that it does represent this variety. Although the type of *Stipa expansa* Poir. is not available for examination, the written diagnosis is also clear that this is var. *trichopodes* (Lamarck 1806). Poiret's Latin diagnosis is unclear concerning the relative size of the spikelet structures. However, his French description mentions that the glumes are almost equal to the floret, which is typical of this variety. *Trichochloa expansa* DC. is based on a different specimen and is synonymous with var. *capillaris* (see also nomenclature under var. *capillaris*). A fragment of *Agrostis arachnoidea* Poir. at US is var. *trichopodes*.

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